

FLAMINGO PREDATION IMPACTS ON BENTHIC COMMUNITIES: EFFECTS OF SPATIAL GRADIENTS

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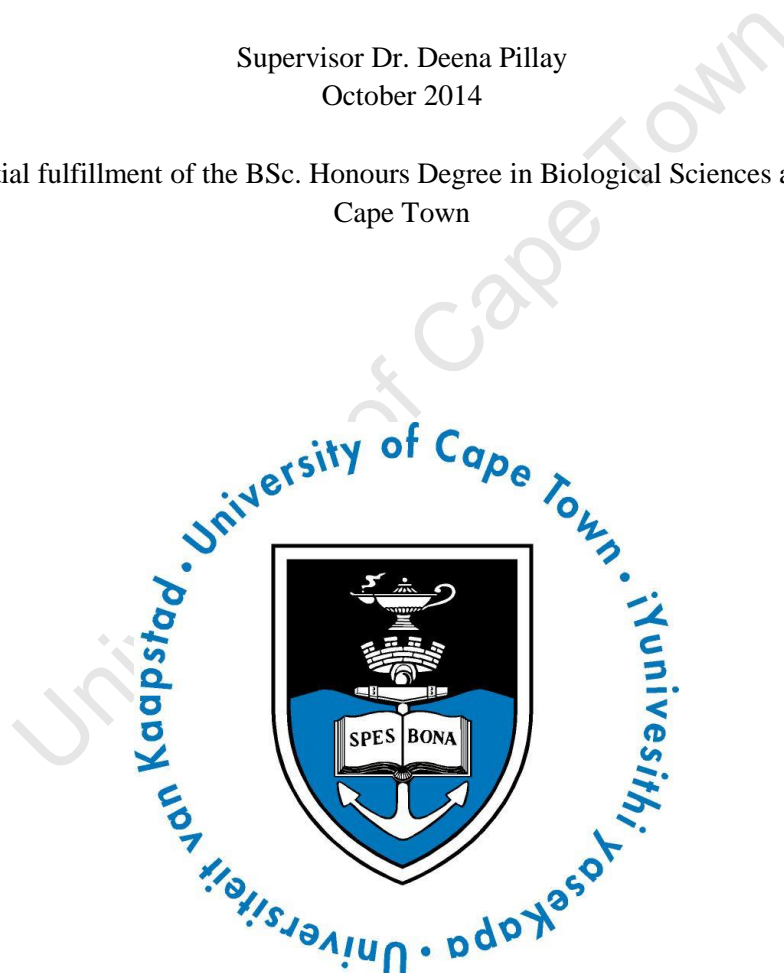
KIRTI GIHWALA

Department of Biological Sciences, University of Cape Town, Private Bag X3, Rondebosch 7701, Cape
Town, South Africa

Supervisor Dr. Deena Pillay

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ABSTRACT

Biological disturbances on marine soft sediment ecosystems have been well researched. However, little attention has been paid to the potential ecological role that iconic shore bird predators may have on marine ecosystems. This paper tests the effects of spatial gradients on Greater Flamingo (*Phoenicopterus ruber*) predation impacts on the benthic macrofaunal community structure in an intertidal sandflat ecosystem in South Africa. *P. ruber* is a benthic filter-feeder known to feed on benthic dwelling invertebrates through pit formation, where deep sediments are stirred up by trampling their feet. Macrofaunal community structure between flamingo pit foraging structures and adjacent non-foraged sediments (controls) yielded insignificant spatial differences. However, subtle positive and negative effects of flamingo predation on macrofaunal abundance were noted at specific sites. Flamingos in this study were not targeting a specific prey group. Thus of the 19 macrofaunal prey items identified, none were significantly impacted across treatments, except for an unidentified polychaete. However, this was once again site specific. The results suggested this polychaete is generally abundant within the area sampled. Furthermore, its distribution is perhaps affected by the level of intensity employed in pit-foraging, rather than being preyed upon. Greater polychaete abundance in pits relative to controls may be attributed to vigorous flamingo feeding efforts. Pit foraging appears to be an expensive strategy to employ, but the energy investment may be reduced through the use of sophisticated sensory organs to detect accessible prey deep within the sediment. Overall, the study has shown that the impact of flamingo predation on a spatial gradient is small and site specific. However, the study highlights the need for further research on quantifying the ecological role flamingos play as predators on marine ecosystems.

KEYWORDS: disturbance, predation, *Phoenicopterus ruber*, community structure

INTRODUCTION

Disturbances are regarded as events that change population biomass through mortality, removal of species, community structure change (Dodson *et al.* 1998) and alteration of resource availability within an environment (Probert 1984). Marine soft-bottom communities are affected by a variety of disturbances (Probert 1984) which in turn play an important role in determining community structure (Thrush *et al.* 1991). Physical factors in the form of storms, tidally induced waves as well as hypoxia generate large scale (km^2) natural disturbances, whereas small scale ($\text{cm}^2\text{-m}^2$) disturbances are created biologically from the activities of marine soft-sediment community residents. Epi- and infauna species such as holothurians and enteropneusts create disturbed patches through sediment processing and thalassinideans excavate burrows. These are common forms of infaunal disturbances (Probert 1984).

Marine-soft sediments are the most common habitat on earth, yet the relative importance of biological forces that structure marine-soft sediment communities are poorly understood (Wilson 1991). Rocky marine shore communities are immensely influenced by competition, where species compete for space. Competition has also been cited as important in marine soft-bottom communities, however, it does not account for community structure adequately in most cases. Predation as a form of biological disturbance has been considered to be a more important process affecting community structure in soft-sediments (Glassom & Branch 1997).

Three categories of predators are recognized in soft-sediment habitats: epi-benthic predators, infaunal predators and sub-lethal browsers. Each predator category has a different influence on the macrobenthic community in terms of net effects on community structure. Epibenthic predators are highly mobile and selective feeders that probe and extract prey from the sediment (Thrush 1999). Small predators such as crabs and rays are well known for excavating pits in the sediment in search

of prey. They not only generate a biological disturbance by removing prey, but also create a physical disruption of natural layering of sediments, resulting in altered topography and local hydrodynamics (Thrush 1999). Such effects can remove residents, alter re-colonization patterns and processes and elevate exposure of prey to secondary predators (Thrush *et al.* 1991). Gray whales on the other hand, are amongst the largest disturbance generators, where they have been reported to produce disturbance patches of 6m² in a 27km littoral sandflat (Weitkamp *et al.* 1992). Several bird species have also been known to impact prey populations, especially when they occur in large numbers (Glassom & Branch 1997). The combination of these disturbances, created from residents and epibenthic predators at various frequencies and intensities, allow for a mosaic of macrobenthic community patches to form at different stages of succession within the soft-sediment environment (Johnson 1970). These are the crucial localized disturbances that generate and enhance spatio-temporal heterogeneity in marine soft-sediment ecosystems (Probert 1984).

Studies have shown that shore bird predation can reduce prey densities on a large scale, and that they could substantially reduce the abundance of invertebrate infauna in muddy substrates (Quammen 1981). Flamingos are colonial birds and occur at high densities at various marine soft-sediment habitats (Rodríguez-Pérez *et al.* 2007). Along with their large size and feeding habits, the presence of flamingos may have important ecological effects in marine ecosystems. The Greater Flamingo (*Phoenicopterus ruber*) occupies coastal and estuarine zones and they are filter feeders, feeding off small invertebrates through their different foraging styles (Rodríguez-Pérez *et al.* 2007). Such techniques include sweeping their bill as they walk along the sediment (to create channels in sediment) or they stamp with their feet, lifting one leg and alternating with the other in rapid succession. While stamping and sinking into the muddy substrate, flamingos create a circle with the use of their bill. These saucer-like depressions are pits created in the sediment (Johnson

& Cezilly 2007). Trampling can produce ring depressions in the sediment up to 1m in diameter. When flamingos occur in large numbers, a vast area of sediment topography can be altered. This has been shown in Namibia, where the sediment properties were changed and benthic invertebrate populations decreased in Walvis Bay and Sandwich Harbour (Glassom & Branch 1997).

Flamingos are iconic birds, however up till now, only descriptive and observational studies have been conducted on these shorebirds. The predatory role of flamingos in an ecological system has rarely been quantified (Bildstein *et al.* 2000). There is a need to understand their role as a predator and their link to the environment, in order to enhance our understanding of disturbances in the form of predation that play a pivotal role in community organization, as no studies have been conducted in South Africa.

In this paper, (1) the predation impacts of the *P. ruber* on the benthic macrofauna community structure in the Heuningnes Estuary, situated in the De Mond Nature Reserve, will be examined; as well as (2) how these impacts are influenced spatially along the length of the system. Core samples of macrofaunal responses will be taken from flamingo foraged and non-foraged sediment. Studies have shown that in winter, during the non-breeding season, flamingos migrate to many staging posts under a South African network of wetlands. These staging posts are regarded as important feeding sites for migratory shorebirds (McCulloch *et al.* 2003). For this reason, winter sampling was conducted.

It was hypothesized that (1) consumption by *P. ruber* will exert a net negative effect on prey assemblages, but that (2) the predation impact on the macrofaunal community will not be influenced spatially.

MATERIALS AND METHODS

Study area

The Heuningnes Estuary is Africa's southernmost estuary (Fig 1A) and is situated at 34°43''S and 20° 00''E and occupies an area of 918ha (Barnes *et al.* 1998). This marine ecosystem extends for 12km across the flat coastal plain area of the Zoentendals Farm. However, only the lower 2km stretch showcases true estuarine properties (Bickerton 1984), where there is much tidal activity resulting in marine salinities. The estuary mouth is an extensive bay consisting of sand, mudflats and tidal saltmarsh (Barnes *et al.* 1998) with a mean sea level of 1.13m. The estuary connects to the Indian Ocean through a double dune ridge at the De Mond Forestry Station. The estuary is characterized by having a Mediterranean climate, with winter rainfall and hot dry summers (Bickerton 1984).

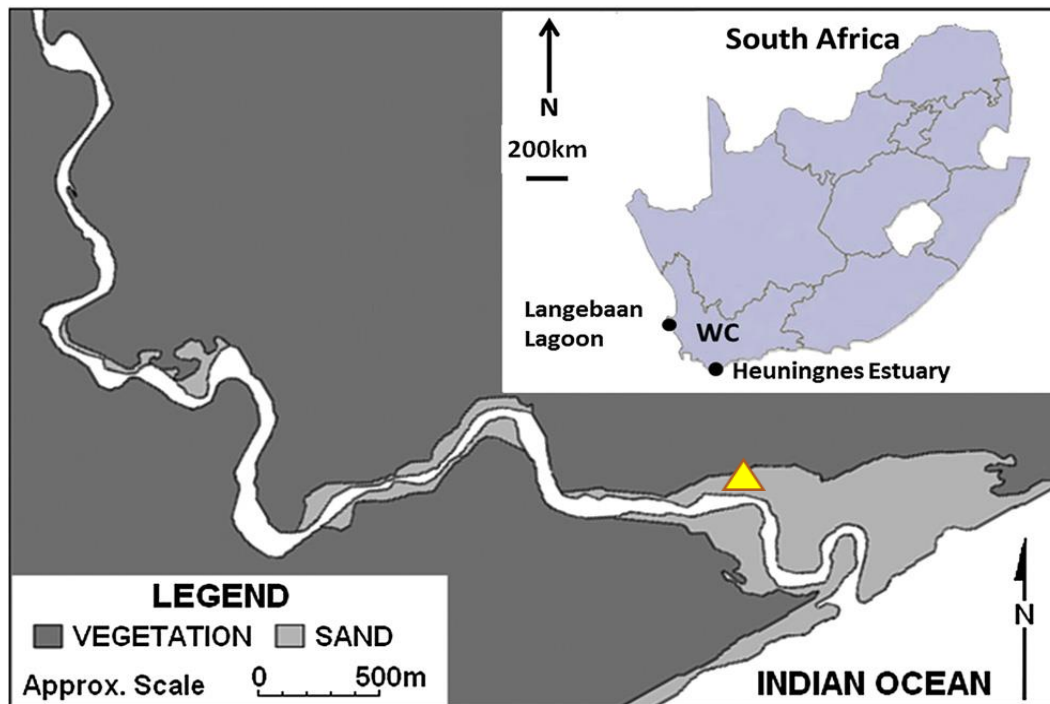


Fig 1A: Map of the Heuningnes Estuary depicting geographical position in the Western Cape (WC) of South Africa. Yellow triangular beacon indicating approximate area where *P. ruber* were predominately feeding (adapted from Kallen *et al.* 2012).

In order to quantify the impact of Greater Flamingo predation on the macrobenthic community along the spatial gradient, macrofauna were sampled in foraging pits and compared with adjacent non-foraged sediments (referred to as controls hereafter). A stretch of intertidal sandflat (Fig 1A), at the lower reaches of the estuary, was observed to be frequently used as a foraging ground by flamingos. This sandflat was divided into four equidistant sites. At each site, one transect from the high to the mid shore was marked. Along which two equidistant quadrats (5m x 5m) were sampled (Fig 1B). Due to time and labour constraints, additional transects per site could not be sampled. Samples were collected during spring low tide on the eastern bank of the estuary. Human presence in the system is low due to restrictions imposed by management authorities. The estuary is permanently open to the sea and a strong estuarine gradient is present (Harrison 2004).

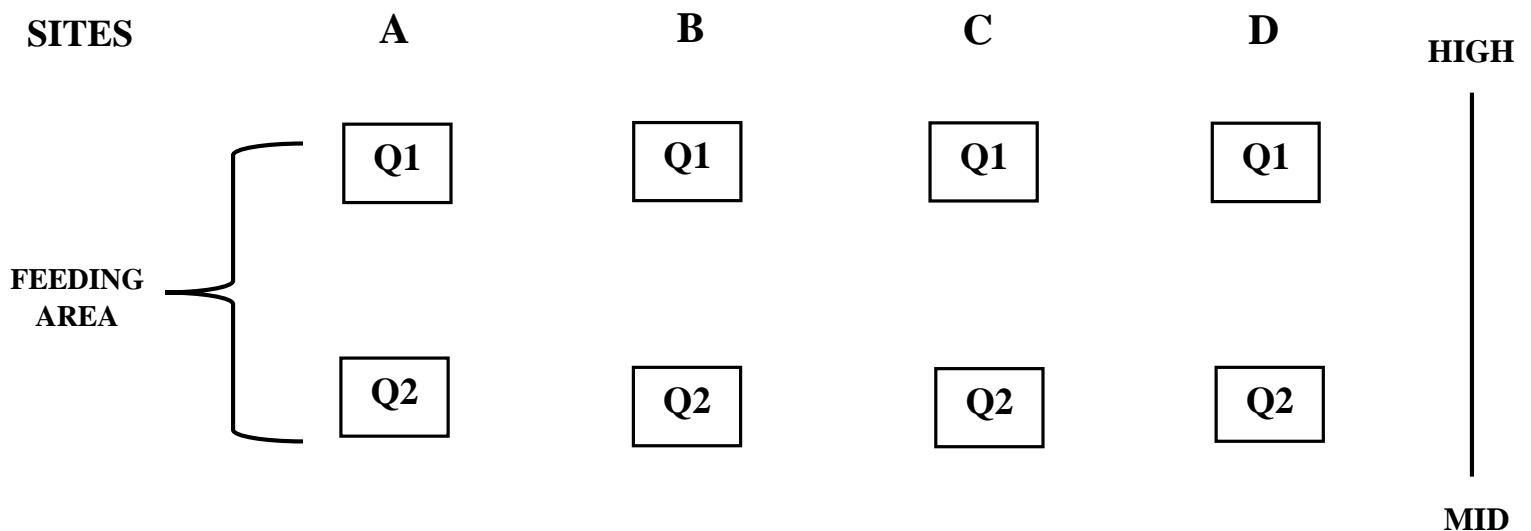


Figure 1B: Sampling design used to sample macrofauna from the high to the mid shore-line within designated area of Heuningnes Estuary.

A total of 48 macrofauna samples were collected, which comprised of three pit samples and three samples for the corresponding feeding structure controls at each of the two quadrats per site. Control samples were collected within 1m from the pits (to reduce variability) where there was no evidence of flamingo foraging. For each pit sample as well as the controls, three cylindrical sediment cores (depth =15cm, diameter =10cm) were collected and pooled into a bucket. Thereafter, the sediment cores were sieved in a 500 μ m mesh five times, followed by a 2500 μ m mesh. All retained material were placed in plastic jars and preserved in 70% ethanol and Rose Bhengal. In the laboratory, macrofauna were sorted, counted and identified.

Statistical Analyses

Multivariate analyses were performed on unstandardized and transformed (fourth-root) abundance data using PRIMER v.6.1.5 (Plymouth Routines in Multivariate Ecological Research; Clarke & Gorley 2006). Non-metric multidimensional scaling (MDS) ordinations, based on resemblance matrices generated from Bray-Curtis similarities, were used to visually assess macrofaunal community structure between pits and their respective controls as well as spatial differences between sites. An Analysis of Similarity (ANOSIM) was performed to test the effects of (1) flamingo predation, (2) site and (3) the interaction of these two factors on macrofaunal community structure. The DIVERSE function was utilized in order to calculate macrofaunal abundance (N), species richness (total number of S), Pielou's evenness index (j) as well as Shannon-Wiener diversity index (H).

SPSS (Statistical Package for Social Sciences) v.22 was utilized for univariate tests. Kolmogorov-Smirnov tests were used to test for normality and homogeneity of variance in data. Data were square-root transformed if they did not meet the required assumptions for parametric testing. Two-factor Analysis of Variance (ANOVA) were conducted to assess whether macrofaunal community

indices differed between pits and controls as well as spatially between sites. The latter tests were also used to test for treatment and spatial differences on the most numerically dominant species.

RESULTS

MDS visually confirmed the lack of differences in community structure between foraged and non-foraged sediment as well as between sites (Fig 2). ANOSIM revealed similar results, indicating there was no difference in community structure between pits and controls ($R = -0.004$, $p = 0.434$) nor between sites ($R=0.018$, $p = 0.189$). The interaction between treatment and site nearly accounted for a significant difference in community structure ($R = 0.057$, $p = 0.056$). Macrofaunal abundance did not statistically differ between foraging structures and controls (ANOVA $F_{1, 40} = 0.624$, $p = 0.434$; Fig 3A) as well spatially across sites ($F_{3, 40} = 1.02$, $p = 0.396$). However, there was a significant interaction between treatment and site that accounted for variability in macrofaunal abundance ($F_{3, 40} = 3.12$, $p = 0.036$). Sites A and B showed a greater macrofaunal abundance in foraged sediment compared to non-foraged sediment. In sites C and D, the opposite effect was noted, as there was a decline in macrofaunal abundance in pits compared to controls. Species richness of macrofauna (Fig 3B) did not differ statistically between foraging structures and controls ($F_{1, 40} = 0.438$, $p = 0.512$), nor between sites ($F_{3, 40} = 0.510$, $p = 0.678$) and there was no significant interaction between treatment and site ($F_{3, 40} = 0.820$, $p = 0.491$). Pielou's evenness index was only significantly influenced by the interaction between treatment and site ($F_{3, 40} = 4.89$, $p = 0.005$; Fig 3C). The same result was recorded for macrofaunal species diversity ($F_{3, 40} = 3.32$, $p = 0.029$; Fig 3D). Both community measures revealed small differences in sites A and C. However, in sites B and D, there were significant differences between pits and controls.

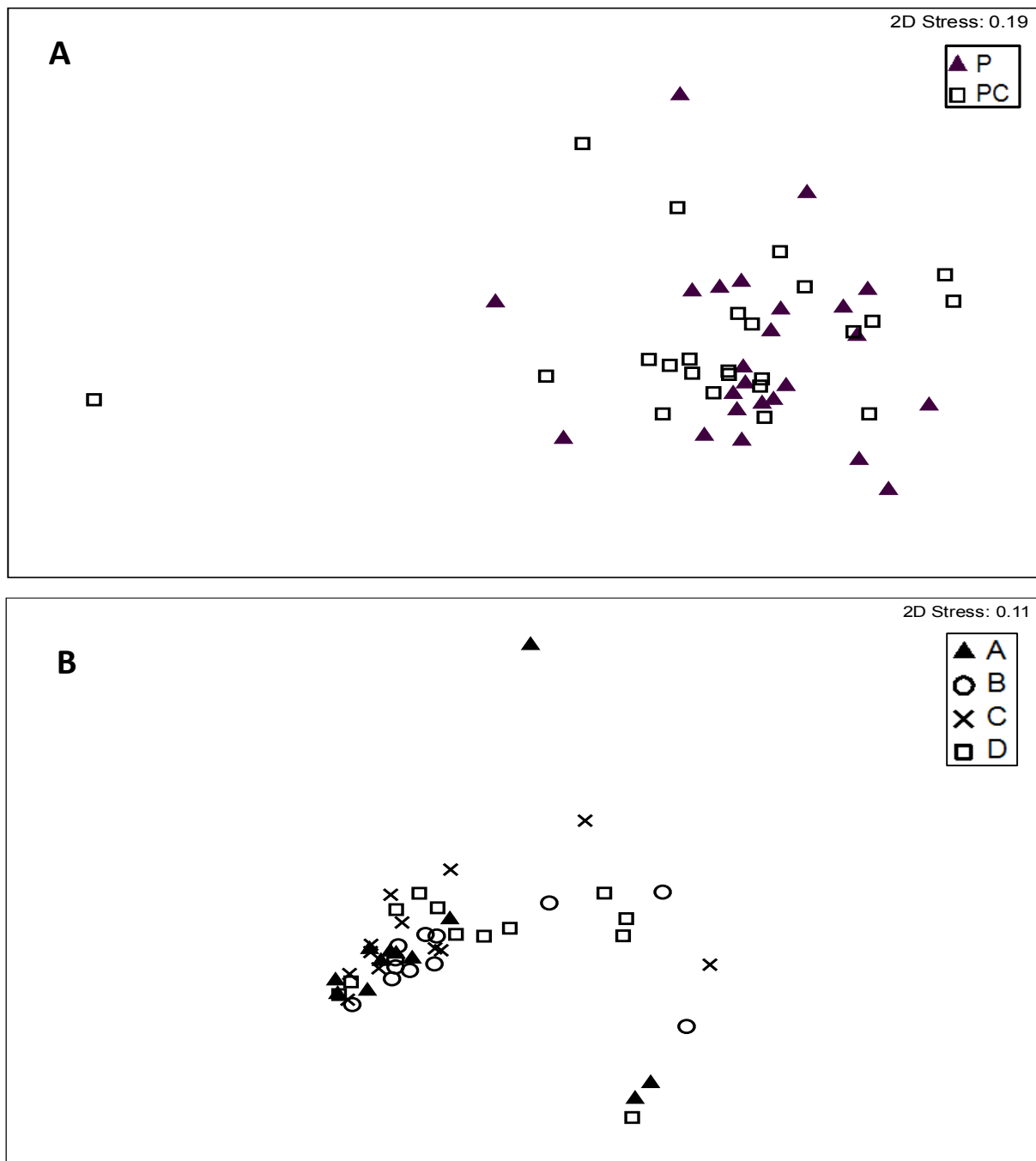


Figure 2: MDS ordination showing differences in macrofaunal community structure between (A) pits and pit controls and (B) sites.

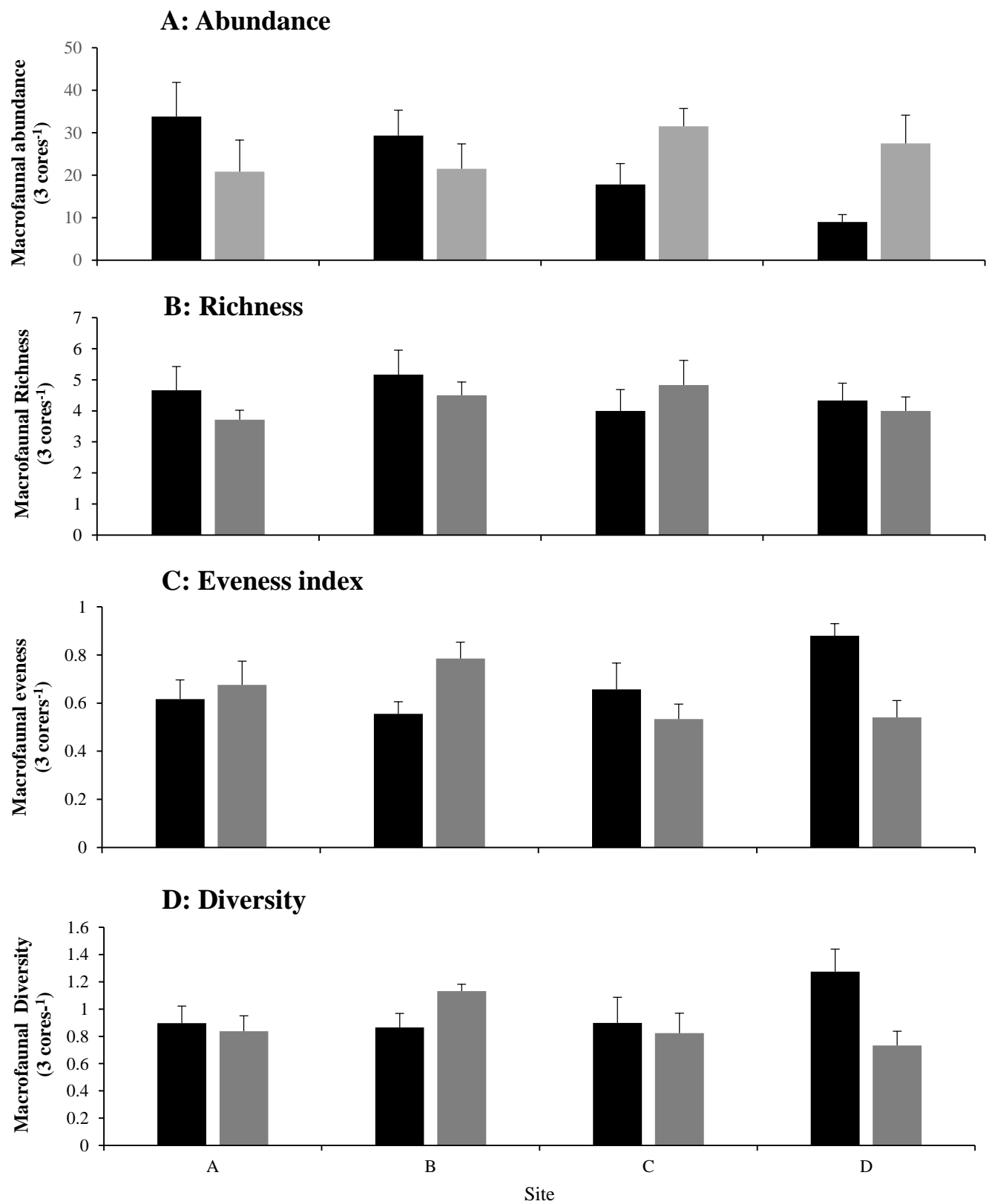
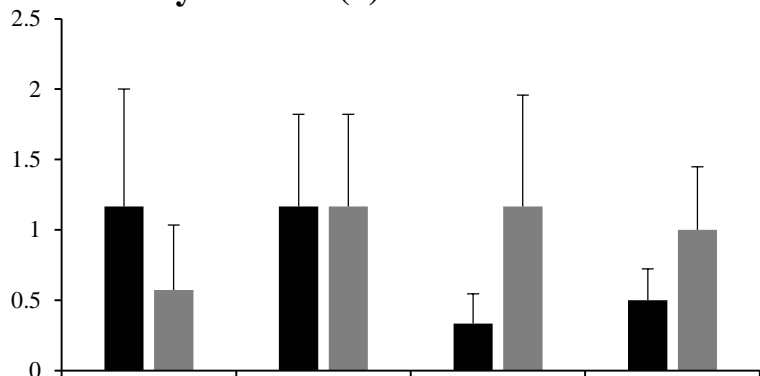


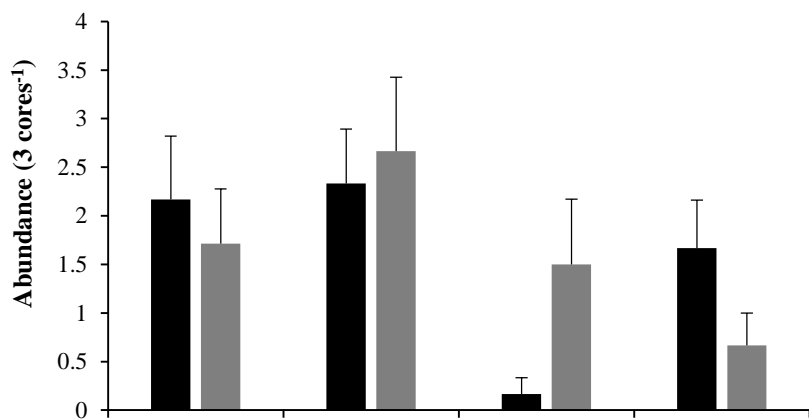
Figure 3: Differences in macrofaunal (A) abundance, (B) richness, (C) evenness index and (D) diversity between flamingo foraging structure (Black) and controls (Grey) at different sites. Means \pm 1SE are shown.

Five dominant macrofaunal species were present in flamingo pits and controls at each site (Fig 4). Juvenile polychaete A (ANOVA $F_{1, 40} = 0.044$, $p = 0.834$) along with the crab *Paratyldiplax blephariskios* ($F_{1, 40} = 0.044$, $p = 0.834$) and Calanoid copepods ($F_{1, 40} = 0.002$, $p = 0.963$) did not differ statistically between pits and controls. There was also no statistical difference between sites for juvenile polychaete A ($F_{3, 40} = 0.326$, $p = 0.807$), *P. blephariskios* ($F_{3, 40} = 1.106$, $p = 0.358$) nor for Calanoid copepods ($F_{3, 40} = 1.426$, $p = 0.249$). Interestingly, the species showed very different response patterns between foraged and non-foraged sediment. Juvenile polychaete B showed no significant difference in abundance between foraging structures and controls ($F_{1, 40} = 0.828$, $p = 0.368$) nor between sites ($F_{3, 40} = 0.742$, $p = 0.534$). However, there was a significant interaction between treatment and site ($F_{3, 40} = 3.82$, $p = 0.017$) for the abundance of polychaete B. The abundance of polychaete B increased in foraged sediment in sites A and B. In contrast, its abundance was decreased in foraged sediment in sites C and D. Tupilid fly larvae did not statistically differ between pits and controls ($F_{1, 40} = 0.012$, $p = 0.914$), but did significantly differ spatially between sites ($F_{3, 40} = 3.671$, $p = 0.020$). In sites A and B, across the treatments, there was a much greater abundance of this species compared to sites C and D.

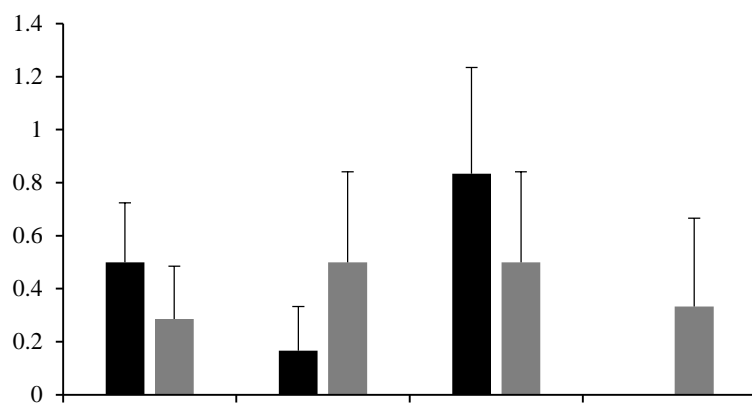
Polychaete A (J)



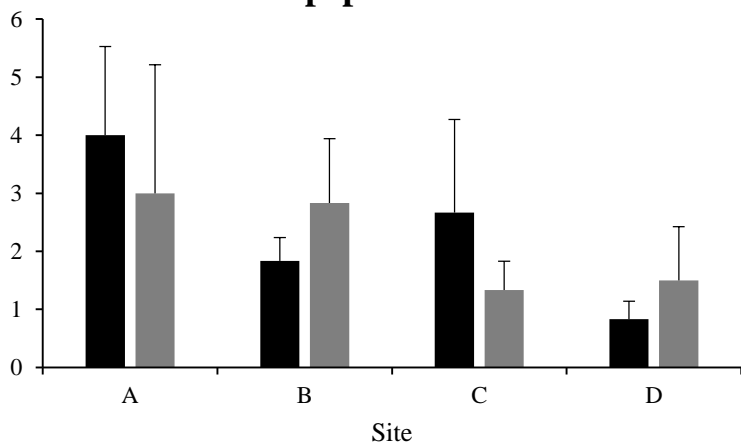
Tipulid fly larvae



Paratyloidiplax blephariskios (J)



Calanoid copepods



Polychaete B (J)

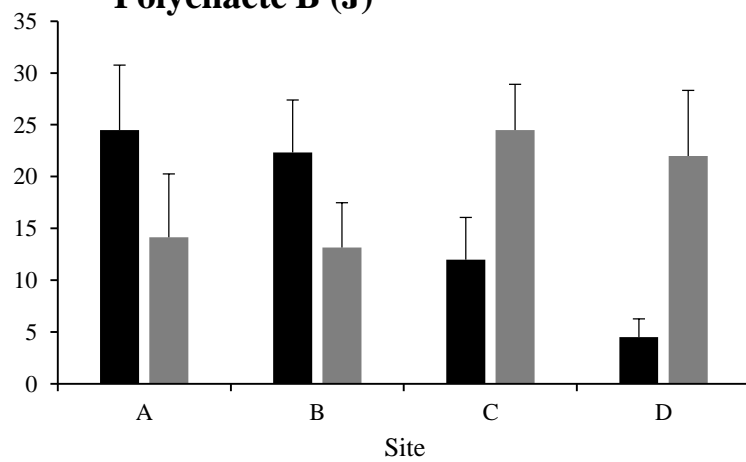


Figure 4: Variation in abundance of macrofaunal species between flamingo foraging structures (Black) and controls (Grey) at different sites. Means \pm 1SE are shown.

DISCUSSION

The aims of this study were to (1) quantify the difference in macrofaunal community structure between flamingo foraged sediment and non-foraged sediment and (2) how these quantified impacts were influenced spatially. However, the central purpose of this study was to gain a better understanding on the ecological role that flamingos play as predators, and the potential effects these biological disturbance agents have on the marine-soft sediment ecosystem, as limited studies have been conducted on these shorebirds (Glassom & Branch 1997).

With the comparison of flamingo pit foraging structures and their controls, it emerged that flamingo foraging effects in macrofaunal assemblages were very subtle. In terms of univariate measures, macrofaunal abundance was not greatly affected. The same result applied spatially across sites. In addition, the interaction between treatment and site did affect differences in macrofaunal abundance even though these were subtle. Macrofaunal evenness along with macrofaunal diversity yielded the same result, despite the latter also being weak. These findings further indicate subtle effects of flamingo predation on the macrofaunal community level.

Although these effects were weak, flamingo predation did exert a top-down control on macrofaunal abundance, as prey were reduced by 43% and 67% in sites C and D respectively. This is interesting, as a review conducted by Peterson (1979) revealed that excluding large predators will effectively increase the macrofaunal density by two to three fold within an intertidal area. However, there are reasons which could possibly explain why this was not the case in the present study. Firstly, Peterson (1979) carried out a global experimental study where he excluded many large epibenthic predators. The current study only observed a single shorebird predator. In addition, there were also discrepancies between the methods utilized in the two studies. Peterson

(1979) conducted a caging experiment, where he physically manipulated the feeding areas for the predators to prey on. The same procedure was not carried out for the present study as it was a field observation, noting where flamingos were feeding naturally, whereby samples were taken accordingly.

It was hypothesized that flamingo predation would result in a net decline of macrofaunal abundance and richness in pit foraging structures relative to their controls. Furthermore, the degree of decline was not hypothesized to magnify spatially between sites. However, results obtained only partially supported the stated hypotheses, as the negative effects did not consistently take place across treatments and sites. Negative flamingo effects were only observed for macrofaunal abundance, species evenness as well as diversity, of which all were site specific. Both species evenness and diversity were negatively affected in foraged sediment at site B. Macrofaunal abundance, as mentioned previously, were strongly reduced only in sites C and D. Remarkably, positive flamingo feeding effects were observed at site D for species evenness and diversity. Macrofaunal abundance on the other hand, increased by 39% and 36% (sites A and B) in pit foraging structures relative to controls. These findings contradict the Namibian study, where Glassom & Branch (1997) concluded that *P. ruber* primarily exerted negative effects on macrofaunal assemblages.

The difference between the findings could be due to different time-scales for each of the studies conducted. Glassom and Branch (1997) measured macrofaunal responses to flamingo predation over a single year, whereas the current study recorded the same responses over four days. In addition, the Namibian study conducted exclusion experiments due to large Greater Flamingo densities residing in Walvis Bay (± 12000) and Sandwich Harbour (> 500). In contrast, only 10-20

flamingos were observed in the present study. These small, short-lived disturbances possibly explain why flamingo pit foraging can generate positive effects on macrofaunal assemblages.

Only 19 macrofaunal species were observed in samples, from which only five occurred regularly between the treatments. However, none showed significant differences in abundance between pits and controls. Only the unidentified polychaete B was observed to be significantly affected, but this was site specific. This once again reveals the subtle effects of flamingo predation on the benthic macrofauna. It is known that a number of physical factors influence macrofaunal community measures. Sediment particle size is one of many environmental factors. A study conducted by McLachlan (1996) revealed that large coarse sands lowers macrofaunal abundance. Sediment characteristics at the mouth of Heuningnes Estuary, on the eastern bank, revealed medium sized coarse particles (Bickerton 1984). Furthermore, since these flamingos were feeding only in the intertidal region, Virnstein (1977) suggested that predation impacts on macrofauna are greater in subtidal rather than intertidal regions, due to the difference in magnitude of macrofaunal densities. Therefore, based on the particle size and tidal height, it is possible that *P. ruber* were predominately feeding off a small pool of macrofauna within the area sampled. This could explain the subtle effects of flamingo predation observed in the present study.

A peculiar observation was made prior to sampling. It was observed that only pit foraging structures were evident within the sampling area. Channel foraging structures were rare. Past studies have shown that creating pits, through stirring up sediments, is an energetically demanding activity (Pennycuick & Bartholomew 1973). The optimal foraging theory states: animals employ a suitable foraging technique, whereby energy invested to search and pursue prey is offset by the energy gained through prey capture (MacArthur & Pianka 1966). By considering this theory, pit foraging does not make sense from an energetics point of view, since there is a low macrofaunal

abundance to feed on. This is based on the particle size and tidal height as mentioned previously (Virnstein 1977; Bickerton 1984). However, it has been noted in studies that as food resources become scarce, predators respond to these environmental limits by expanding their choice of prey (Pyke *et al.* 1977). This theory is supported in the present study, as there was no significant difference in species richness between pits and controls, indicating that flamingos were not targeting a specific prey group.

Generally, the main selection of prey items for Greater Flamingos is determined by specific mesh sizes. The distance between the bill lamellae serves as the mesh measurement. Favourable prey sizes are retained in the mesh to be consumed, whereas sizes that are too small or large are rejected and returned to the sediment (Jenkin 1957). Studies have shown that *P. ruber* are bottom feeders (Brown 1959) and feed mainly on polychaetes, copepods, chironomids, insect larvae and even organic matter imbedded in muddy sediments (Brown *et al.* 2005). The present study supported some of the prey items that were found in flamingo pit foraging structures. However, the main contributor to the macrofaunal abundance at each designated site, was the unidentified polychaete B. As mentioned previously, positive effects of pit foraging were observed in sites A and B. Regardless of the duration and density of the predatory disturbance, pit foraging can generate positive effects due to the mechanism employed. This responsible mechanism involves sediment-reworking in the form of an upward conveyor belt bioturbation (Francois *et al.* 1997). By mobilizing the sediment through their footwork, nutrients are known to increase upon their release into the water column (Comin *et al.* 1997). This subtle effect from pit foraging may possibly explain the increase in other species abundance in pits relative to non-foraged sediment. With regard to polychaetes, studies have shown that this taxon is generally found in the upper 5-10cm sediment layer above the undisturbed mud sediments. Therefore, it is possible that as flamingos

stamp-feed in a circular pattern, they are able to stir up polychaetes from the deep sediments and place them to the upper surface layers (Bilstein *et al.* 1991). This may imply that at sites A and B flamingos were feeding vigorously, leading to greater densities of polychaete B being upwelled from deeper sediments. In contrast, a less intense pit foraging activity may have been conducted at sites C and D. It was observed that polychaete B displayed consistently greater densities, in comparison to the rest of the macrofaunal species identified across treatments and sites. This reveals that the unidentified specimen is generally abundant in the sampling area and may not necessarily be preyed upon, yet remains affected by the degree of intensity employed in pit-foraging.

Cramp *et al.* (1997) have observed that many flamingos tend to feed in small concentrated areas over a long time period. Ornithologists have found flamingos have olfactory bulbs (Bang & Cobb 1968) and may possess pressure sensors in their bill (Jenkin 1957). By utilizing these sophisticated sensory organs, flamingos, like other predators, can reduce energy investment in search of prey. This may support why flamingos foraged in a small area in the present study, due to the strong detection of catchable prey beneath the sediments. However, whether these flamingos are obtaining their nutritional requirements is questionable, as studies have shown that during the non-breeding seasons juvenile flamingos feed less than their adult counterparts (Espino-Barros & Baldassarre 1989). In addition, non-breeding flamingos have a greater feeding activity at night compared to the day (Britton *et al.* 1986). Therefore, this may have influenced the day time sampling of macrofaunal responses.

Overall, *P. ruber* densities and spatial predation impacts at Heuningnes Estuary are minimal and site specific. Flamingo pit-foraging has shown positive and negative disturbance effects, which in turn may influence spatial-temporal heterogeneity in intertidal sandflats. However, the study has provided insight and a step forward for future research on a charismatic shorebird predator, of which little attention has been paid toward its ecological role in marine systems (Glassom & Branch 1997).

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REFERENCES

- Bang BG, Cobb S (1968) The Size of the Olfactory Bulb in 108 species of Birds. *The Auk* **85(1)**: 55-61
- Barnes KN, Johnson DJ, Anderson MD, Taylor PB (1998) Important Bird Areas in Africa and associated islands – South Africa. pp 793-876
- Bickerton IB (1984) Heuningnes (CSW19) CSIR, National Research Institute for Oceanology. 73pp
- Bildstein KL, Frederick PC, Spalding MG (1991) Feeding Patterns and Aggressive Behavior in Juvenile and Adult American Flamingos. *The Condor* **93(4)**: 916-925
- Bildstein KL, Baldassarre GA, Arengo F (2000) Flamingo science: current status and future needs. *Waterbirds: The International Journal of Waterbird Biology* **23**: 206-211
- Britton RH, de Groot ER, Johnson AR (1986) The daily cycle of feeding activity of the greater flamingo in relation to the dispersion of the prey Artemia. *Wildfowl* **37(37)**: 151-155
- Brown LH (1959) Flamingoes in Africa. *Journal of African Ornithology* **30**: 79-83
- Brown C, King C (2005) *Flamingo husbandry guidelines*. American Zoo and Aquarium Association. Silver Spring: Maryland, 352pp
- Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth
- Comin FA, Hernandez O, Romero JA (1997) The effect of the foraging activity of a non-breeding flamingo population on the macroinvertebrate community in a coastal lagoon. In *Yucatán a través*

de los siglos: memorias del simposio del 49o Congreso Internacional de Americanistas. Quito, Ecuador, **5**: 61-68

Comin FA, Herrera JA, Martin M (1997). Flamingo footsteps enhance nutrient release from the sediment to the water column. *Wetlands International Publication* **43**: 211-228

Cramp S, Simmons KEI, Ferguson-Lees IJ and the rest. (1997). *Handbook of the birds of Europe, the Middle East and North Africa*. Oxford University Press. Oxford, 722pp

Dodson SI, Allen TFH, Carpenter SR, Ives AR, Jeanne RL, Kitchell F, Langston NE, Turner MG (1998) *Ecology*. Oxford University Press, New York. 434pp

Espino-Barros R, Baldassarre G (1989) Activity and habitat-use patterns of breeding Caribbean Flamingos in Yucatan, Mexico. *Condor* **91**: 585-591

Francois F, Poggiale JC, Durbec JP, Stora G (1997) A new approach for the modelling of sediment reworking induced by a macrobenthic community. *Acta Biotheoretica* **45**: 295-319

Glassom D, Branch GM (1997) Impact of predation by greater flamingos *Phoenicopterus ruber* on the macrofauna of two southern African lagoons. *Marine Ecology Progress Series* **149(1)**: 1-12

Harrison TD (2004) Physico-chemical characteristics of South African estuaries in relation to the zoogeography of the region. *Estuarine, Coastal and Shelf Science* **61**: 73-87

Jenkin PM (1957) The Filter-Feeding and Food of Flamingoes (Pheonicopteri). *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **240(674)**: 401-493

- Johnson RG (1970) Variations in diversity within benthic marine communities. *American Naturalist* **104(937)**: 285-300
- Johnson A, Cezilly F (2007) *The Greater Flamingo*. T & AD Poyser, London UK, 328pp
- Kallen J, Muller H, Franken ML, Crisp A, Stroh C, Pillay D, Lawrence C (2012) Seagrass-epifauna relationships in a temperate South African estuary: Interplay between patch-size, within-patch location and algal fouling. *Estuarine, Coastal and Shelf Science* **113**: 213-220
- MacArthur RH, Pianka ER (1966) On optimal use of a Patchy Environment. *The American Naturalist*. **100(916)**: 603-609
- McCulloch G, Aebischer A, Irvine K (2003) Satellite tracking of flamingos in southern Africa: the importance of small wetlands for management and conservation. *Oryx* **37(4)**: 480-483
- McLachlan A (1996) Physical factors in benthic ecology: effects of changing sand particle size on beach fauna. *Marine Ecology Progress Series*. **131**: 205-217
- Pennycuik CJ, Bartholomew GA (1973) Energy budget of the Lesser Flamingo (*Phoeniconaias minor* Geoffroy). *African Journal of Ecology* **11**: 199-207
- Peterson CH (1979) Predation, competitive exclusion and diversity in the soft-sediment benthic communities of estuaries and lagoons. In: Livingstone RJ (ed) *Ecological processes in coastal and marine systems*. Plenum Publishing. New York, p 233-264
- Probert PK (1984) Disturbance, sediment stability, and trophic structure of soft-bottom communities. *Journal of Marine Research* **42(4)**: 893-921
- Pyke GH, Pulliam HR, Charnov EL (1977) Optimal Foraging: A Selective Review of Theory and Tests. *The Quarterly Review of Biology* **52(2)**: 137-154

Quammen ML (1981) Use of exclosures in studies of predation by shorebirds on intertidal mudflats. *Auk* **98**: 812-817

Rodríguez-Pérez H, Green AJ, Figuerola J (2007) Effects of Greater flamingo *Phoenicopterus ruber* on macrophytes, chironomids and turbidity in natural marshes in Doñana, SW Spain. *Fundamental and Applied Limnology* **170(2)**: 167-175

Thrush SF, Pridmore RD, Hewitt JE, Cummings VJ (1991) Impact of ray feeding disturbances on sandflat macrobenthos: do communities dominated by polychaetes or shellfish respond differently? *Marine Ecology Progress Series*. **69(3)**: 245-252

Thrush SF (1999) Complex role of predators in structuring soft-sediment macrobenthic communities: Implications of changes in spatial scale for experimental studies. *Australian Journal of Ecology* **24(4)**: 344-354

Virnstein RW (1977) The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* **58**: 1199-1217

Weitkamp LA, Wissmar RC, Simenstad CA, Fresh KL, Odell JG (1992) Gray whale foraging on ghost shrimp (*Callinassa californiensis*) in littoral sand flats of Puget Sound, USA. *Canadian Journal of Zoology* **70(11)**: 2275-2280

Wilson WH (1990) Competition and predation in marine soft-sediment communities. *Annual Review of Ecology and Systematics* **21**: 221-41